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FOSSIL AMPHIBIANS FROM QUARRY NINE

by

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The original intention of this investigation was to determine the identity of *Eobatrachus agilis* Marsh. It was soon evident to us, as to other workers, that the type materials represented more than one species. Fragments referred to this form by Moodie (1912, 1914) represent an ilium of a reptile, a femur of a salamander, an unidentifiable fragment of a tibiofibula of a frog and two distinctly different types of frog humeri. Unavailable to us at this time are the vertebra and urostyle illustrated but not discussed by Moodie (1914). Marsh (1887) described this form in the following words: "More recently, various bones of small, anourous amphibians (*Eobatrachus agilis*) have been found, the first detected in any Mesozoic formation." Moodie (1912) described Marsh's material and selected the larger humerus as the type (Yale Peabody Museum no. 1862). He stated that the elements represented a form close to *Bufo* and later (1914) actually placed it in the Bufonidae. Simpson (1926 a and b) merely records the presence of a modern frog in the fauna.³ The importance of these specimens is that the frog remains are among the oldest known and the salamander is the earliest record of that group. Appli-

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³ Reig (1957) for unknown reasons referred *Eobatrachus* to the Discoglossidae.

cation of names to such fragmentary material is in part a matter of taste, but the antiquity of the material and its close correspondence to modern forms make it useful to place the material within the established system of classification.

The senior author is responsible for the sections dealing with anurans; the junior author for the remainder of the specimens.

Class Amphibia
Superorder Salientia
Order Anura
Suborder Aglossa?
Family *incertae sedis*
Eobatrachus agilis Marsh
Plate 1, figs. 1, 3, 5

Holotype: Yale Peabody Museum no. 1862, the distal portion of a humerus.

Locality: Quarry 9, Como Bluff, Wyoming.

Diagnosis: Distinguished from all known frog humeri by the following combination of characters: A) base of the shaft of the humerus perpendicular to the main axis of the humeral ball (*eminentia capitata* of Gaupp, 1894, henceforth referred to as the ball), B) a deep triangular fossa present (*fossa cubitus ventralis*) at the upper end of the ball, C) the ball a fully developed spherical articulating surface which is proportionately large in size, D) a small olecranon scar which is nearly triangular in form but with its apex nearest the lateral border of the humerus, E) weakly developed epicondyles, the medial epicondyle larger than the lateral epicondyle but reduced in size as compared to other frogs, F) narrowest cross-section (or neck) of the humerus is just above the ball.

Description: A broken distal portion of a right frog humerus measuring 6 mm. in length. On its distal portion is a completely rounded but abraded ball, with a diameter of 2 mm. The medial epicondyle is a small slightly abraded nubbin medial to the ball. On the opposite side of the lateral epicondyle is a slight ridge with no evident rise or mound. From the two epicondyles, two distinct ridges run proximally on the main

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shaft of the humerus. Lying between the two ridges is a distinct fossa (*fossa cubitus ventralis*) which is roughly triangular. The base of the triangular pit is formed by the ball and its deepest area is on the medial side above the ball. It gradually becomes shallower both proximally and laterally. The apex of the triangular fossa is rounded and lies midway between the two epicondyles. The lateral surface of the medial epicondyle forms a weak flange which projects slightly medially. The olecranon scar, on the posterior surface of the ball, is a small triangular area whose apex is the same height as the ball and lies midway between the two epicondyles. The neck of the humerus (the area of smallest cross-section) is apparently long and begins far above the ball. There are no indications of a ventral ridge or crest on the neck of the humerus. Comparisons of the fossil with living frogs are based on the following genera: (Unless otherwise indicated only one species of each genus has been examined.)

Leiopelma, *Ascaphus* (Leiopelmatidae); *Pipa*, *Xenopus* (Pipidae); *Discoglossus*, *Barbourula*, *Bombina*, *Alytes* (Discoglossidae); *Rhinophrynus* (Rhinophrynidae), *Pelobates* (2 species), *Scaphiopus* (3 species), *Megophrys* (3 species) (Pelobatidae); *Pelodytes* (Pelodytidae); *Leptodactylus* (2 species); *Batrachophryne*, *Calyptocephalella*, *Eupsophus*, *Physolaema*, *Telmatobius*, *Ceratophrys*, *Eleutherodactylus*, *Pleurodema*, *Adelotus*, *Kyarranus*, *Limnodynastes*, *Lechriodus*, *Helioporus*, *Rhinoderma* (Leptodactylidae); *Dendrobates* (2 species), (Dendrobatidae); *Atelopus* (Atelopodidae); *Bufo* (25 species), *Ansonia*, *Nectophrynoides* (Bufonidae); *Hyla* (10 species), *Acris*, *Gastrotheca* (2 species), *Diaglena*, *Smilisca* (3 species) (Hylidae); *Pseudis* (Pseudidae); *Rana* (5 species), *Arthroleptides* (Ranidae); *Phrynomerus* (Phrynomeridae); *Astylosternus*, *Dyscophus*, *Probreviceps*, *Kaloula*, *Uperodon*, *Gastrophryne* (Microhylidae); *Hyperolius*, *Rhacophorus*, *Megalixalus* (Hyperoliidae).

Discussion: The humerus of anurans is one of the most easily identifiable structures because of the presence of the prominent ball on the distal end. The basic morphology of the humerus is discussed by Gaupp (1894) and the terminology to be followed will be based on this work. Unfortunately this classic

study is based only on members of the genus *Rana* and therefore many described features of the humerus are characteristic only of that family or even that genus. The main aspects of the morphology of the humerus are amply illustrated in Figures 39-41 of this work. The discussion will be restricted to the distal portion of the humerus. On either side are two epicondyles, the *lateral* and the *medial*. In most frogs the medial is larger and more prominent, whereas the lateral epicondyle is usually small or represented by a slight nubbin. Immediately above the ball there may be a slight or relatively deep depression, the *fossa cubitis ventralis* (Gaupp 1894, hereafter referred to as the fossa). On the posterior surface of the humeral ball there is almost always a roughened triangular area which will be called the *olecranon scar*. This represents the area which articulates with the olecranon process of the radio-ulna. Immediately above the widened distal end of the humerus, there usually is a neck region which generally has the narrowest diameter of the entire humerus. On the proximal end of the humerus of almost all frogs there is a *crista ventralis* (Gaupp 1894). In many frogs this ridge is quite long and extends onto the neck of the humerus but usually it is absent on the neck region.

On the basis of morphology the humerus of *Ascaphus* and *Leiopelma* have much in common. There is a distinct fossa and reduced epicondyles in *Leiopelma*. *Eobatrachus* can readily be distinguished from *Leiopelma* by the more advanced structure of the ball. *Ascaphus* has a modern type of ball but the fossa is very small and shallow. The nature of the fossa and the expanded lateral and medial epicondyles and their flanges distinguish it readily from *Eobatrachus*. The Pipidae is characterized by a small but well developed ball, with equally developed epicondyles and a deep triangular fossa. The symmetry of the pipid fossa is much greater than that of *Eobatrachus* but the fossa is relatively better developed than in any other known living or fossil frog. The ball of *Eobatrachus* is much more advanced than either genus although the reduction in size in the pipids may be due to aquatic adaptation and reduction of jumping abilities. The Discoglossids are precluded from relationship to *Eobatrachus* by the lack of the fossa. Other features are characteristic of the Discoglossidae

which eliminate them from further discussion. The Pelobatidae and the Pelodytidae can be eliminated because there is no sign of the fossa (except a tiny fossa-like depression in *Megophrys*) and the apex of the olecranon scar tends to lie laterally rather than medially. The condition of the humerus among the leptodactyloid frogs (including Leptodactylidae, Dendrobatidae, Atelopodidae, Rhinodermidae following Griffith, 1959) is most variable with the single exception that the fossa is never present except weakly in *Batrachophrynus*, which differs from *Eobatrachus* by the presence of a low ventral crest on the neck region (*crista ventralis*) and reduced medial epicondyle in the living species. The Pseudidae and Centrolenidae may be differentiated from *Eobatrachus* in the same manner as the other leptodactyloid families. The bufonids can be easily distinguished by the complete lack of the fossa, the generally curved humerus and by the apex of the olecranon scar being more laterally than medially oriented. The distal portion of the humerus of Hylidae is variable, but is usually characterized by the complete lack of a fossa or at best a lunate deep trench just above the proximal border of the ball. The medial epicondyle is usually moderately or weakly developed and the lateral epicondyle is variable in size from very small to very large. The ranid humerus can be distinguished from the fossil by the small pit-like fossa which lies just above the ball, very prominent medial epicondyle, laterally oriented apex of the olecranon scar, and by the general curvature of the humerus. The phrynomerid humerus is distinguished by its very small ball, elongate diaphysis, and reduced olecranon scar. The fossa in this form is very shallow, triangular, and extremely short. Both the Ranidae and Hyperoliidae have a deep fossa just above the proximal end of the ball. This fossa is distinctly different in its form from those of *Eobatrachus*. It appears that in both of these families the depression may merely be formed by enlargement of the sphere-like pattern of the ball. Both these families also differ from the fossil by the great development of lateral extensions or flanges from the epicondyles, the relatively large size of the medial epicondyle and the lateral position of the olecranon scar.

From the above discussion it appears that there is no clear

relationship between *Eobatrachus* and any of the living families of frogs. The large size of the ball, the development of the fossa, the reduced medial epicondyle, the shape and form of the olecranon scar and the perpendicular position of the humeral shaft all indicate a unique association of characters not found in any living or fossil frog seen. The only frogs which approach *Eobatrachus* as far as the development of the fossa is concerned are the Pipidae and perhaps *Leiopelma*. In all of these the fossa is a symmetrical trough which is not the case in *Eobatrachus*. In both *Xenopus* and *Pipa* the humeral ball is very small with relatively large epicondyles, whereas in *Eobatrachus* the humeral ball is very large and the epicondyles are reduced. Certainly as far as the ball is concerned the humerus is an advanced structure but the development of the fossa may indicate a more primitive condition. The assignment of *Eobatrachus* to Montsechobatrachidae is at best a guess and perhaps it should be considered a more advanced frog than that. Validity of the assignment of *Eobatrachus* to this family (Romer 1945) cannot be determined from the published material of *Montsechobatrachus*.

Superorder Salientia

Order Anura

Suborder Neobatrachia

Family *incertae sedis*

Comobatrachus acnigmati, new genus and species

Plate 1, figs. 2, 4, 6

Holotype: Yale Peabody Museum No. 1863, the distal portion of a frog humerus.

Locality: Quarry 9, Como Bluff, Wyoming.

Diagnosis: Distinguished from *Eobatrachus* by its shallower, symmetrical triangular *fossa cubitus ventralis* and less developed medial epicondyle; similar to some leptodaetylid, microhylid and hyperoliid frogs in the presence of the *fossa cubitus ventralis*, but distinguished from these groups by the poorly developed medial epicondyle, the medial position of the apex of the olecranon scar and straight shaft of the base of the humerus.

Description: A broken distal portion of a right frog humerus measuring 5 mm. long. At the distal end of the fragment there is a large distinct abraded ball (*eminentia capitata*) which has a diameter of approximately 1.3 mm. On the medial side there is a small indistinct slightly abraded medial epicondyle and on the opposite side there is no distinct evidence of a lateral epicondyle. The surface of the area of the lateral epicondyle is slightly abraded. The area of each epicondyle forms slight rounded ridges which meet at the base of the neck. Between the two ridges is a fossa the shape of an isosceles triangle whose base is the upper end of the humeral ball. The fossa is shallow; the deepest area being at the upper border of the humeral ball. Posteriorly, the olecranon scar is triangular in form and its apex is slightly higher than the humeral ball. The apex lies midway between each epicondyle. The neck of the humerus is relatively low and begins above the expanded distal end of the bone.

Discussion: The relationships of *Comobatrachus* are apparently with the more modern frog families. The development of the ball and the general shape of the fossa indicate no relationship to Leiopelmatidae, Pipidae, Discoglossidae, or Pelobatidae. Among the Neobatrachia the Bufonidae, Atelopodidae, Dendrobatidae, Pseudidae (and other groups now placed in the Leptodactylidae by Griffith, 1959) and Hylidae are precluded from consideration by either the complete lack of a fossa or only the slightest indication of such a structure. The fossa of the Ranidae is merely a lunate cleft above the humeral ball. Among the Hyperoliids there is no fossa in *Rhacophorus* or *Megaliaxalus* but a distinct one in *Hyperolius*. The base of the humerus of *Comobatrachus* bears a distinct resemblance to *Eupsophus* (Leptodactylidae), *Hyperolius* (Hyperoliidae), *Probreviceps* and *Kaloula* (Microhylidae). There are distinct differences between the aforementioned modern frogs and *Comobatrachus*. In all the modern frogs the medial epicondyle is better developed and the fossa is distinctly shorter than in the fossil. As a result of these comparisons there is apparently no family of living frogs to which *Comobatrachus* can be assigned, though it appears to be a member of the more advanced families of the Neobatrachia (Reig 1958). It is probable that the

medial epicondyle has been eroded or broken away and if so the humerus would perhaps conform more closely to one of the above genera. Assuming that the epicondyle has not been too badly damaged, it would appear that no family of living frogs would include the features of *Comobatrachus*. Therefore we can only conclude that it represents one of the more advanced families, possibly something related to the more generalized Leptodactylidae or perhaps a family as advanced as the Microhylidae or Hyperoliidae. On the basis of probability a leptodactyloid affinity appears more likely.

Order Urodela

Family *incertae sedis*

Comonecturoides marshi, gen. et. sp. nov.

Plate 2, figs. 3, 4; Plate 3, fig. 6

Holotype: Yale Peabody Museum 3919, complete right femur.

Type locality: Quarry 9, Como Bluff, Wyoming.

Diagnosis: Distinguished from living salamanders principally by the presence of endochondral ossification and heavier ossification of the perichondral diaphysis.

Description: The femur is characteristically urodele, with narrow diaphysis, expanded and unossified proximodistal extremities, and tiny, anteroventral twiglike trochanter. The head in cross section is rounded dorsally, and has a slight ventro-posterior angle. The tip of the trochanter is missing, and the point of separation of shaft and trochanter is about one millimeter distal to the preserved proximal edge of the head. The trochanter is continued on the diaphysis by a crest which diminishes distally, but remains discrete almost to the preserved distal edge of the bone. The dorsal surface of the distal end is swollen and pitted for ligamentary attachment. Ventrally the distal end bears two tiny foramina. The outline of the distal end is oval, slightly concave ventrally and convex dorsally. In cross section, the bone of the shaft is quite thick and there is endochondral ossification within the expanded extremities. Maximum length of femur, 11.5 mm.; maximum

diameter of distal extremity, 3 mm.; maximum diameter proximal end, 2.3 mm.

Discussion: Femora and humeri of urodeles may be distinguished easily by the following characters. In cross section, the distal end of the femur is always convex dorsally and concave ventrally; both dorsal and ventral edges are convex in humeri, giving a lobate appearance. The humeri always possess a strong bladelike crest ventrally, continuous with the head, and a smaller trochanter is sometimes present dorsally (e.g. in Salamandridae, see Francis 1934, pl. 7, fig. 42). Femora of living families of urodeles are quite distinct, particularly with respect to the outline of the head in cross-section, and to a lesser degree the shape and orientation of the trochanter. The outline of the distal extremity is less characteristic but may also be helpful. Plate 3 shows outlines of femoral heads of all families (except Sirenidae which lack hind limbs) of living urodeles. Each drawing is based on several specimens and is intended to reflect the characteristic shape for each family rather than that of any particular individual. The following material was seen: (numbers in parentheses indicate specimens examined)

Ambystomidae

- Ambystoma tigrinum* (3)
A. opacum (1)
Rhyacotriton olympicus (1)
Siredon mcxicanum (1)

Hynobiidae

- Hynobius stejnegeri* (1)
Batrachuperus pinchonii
 (1)

Cryptobranchidae

- Andrias scheuchzeri*
japonicus (4)
Cryptobranchus
alleganiensis (1)

Salamandridae

- Salamandra atra* (2)
S. maculosa (1)
Mertensiella caucasica (1)
Taricha granulosa (1)

Amphiumidae

- Amphiuma tridactylum* (3)
A. means (1)

Proteidae

- Proteus anguinus* (1)

Necturidae

- Necturus maculosus* (4)
N. punctatus (1)
N. beyeri (1)

Plethodontidae

Plethodon cinereus (2)

Leurognathus

marmorata (1)

Desmognathus fuscus (2)

Pseudotriton ruber (1)

The shape of the head of the femur was found to be relatively constant in all families except Ambystomidae. *Rhyacotriton* resembles *Ambystoma*, both differ from *Dicamptodon ensatus*. The proximal ends of femur and humerus are difficult to distinguish in *Siredon mexicanum*, probably due to lack of ossification. Comparison of the figures will show that the closest resemblance to the Como Bluff specimen is with *Necturus* (considered here as a family separate from *Protens*, following Hecht 1957). There is some similarity to *Amphinma*, from which it is distinguished by the less sloping posterior border of the head and the slightly different angulation of the trochanter. Characters of the shaft, trochanter, and distal end are shown in Plate 2. Ambystomids have a relatively divergent trochanter, often connected proximodistally to the shaft by thin crests or webs of bone. The short stubby femur of the cryptobranchids with its blunt trochanter is easily recognizable, and the outline of the distal end is especially characteristic. Salamandrids often have ossified extremities and the trochanter is falcate with a rounded excavation between trochanter and head. This condition is also found in plethodontids, though they may be separated by the proximal outline of the head. *Protens* has a very reduced femur, with only a tiny ridge instead of a trochanter. Necturids are characterized principally by the rounded outline of the femoral head, which lacks any prominent crests or angles, and in this respect *Comonecturoides* most closely resembles this family. Comparison with *Necturus beyeri* and especially *N. punctatus* was difficult due to reduced ossification in limb extremities of these forms. Both of these species show a little more anteroposterior compression of the head of the femur than does *N. maculosus*, but this is in part due to lack of ossification in the most proximal part of the shaft. In perennibranchiate or larval types

only the larger specimens or species are well ossified enough for comparison.

Interrelationships of the various families based on the outline of the femoral head are as follows. The similarity is greatest between hynobiids and *Ambystoma*, to be expected due to the close relationship between the two groups. The salamandrid outline is easily derived from this type as is the plethodontid. The necturid outline is probably closer to the hynobiid or perhaps the salamandrid than to any of the others (the latter relationship suggested by Noble (1931) on the basis of reproductive structures) and the similarity of *Amphiuma* (probably a salamandroid derivative) to *Necturus* may strengthen this suggestion, though of course no particular weight may be placed on this single character. The stubby outline of the cryptobranchid femur is unlike any other.

Class Reptilia

Order Sauria?

Plate 1, figs. 7, 8

Yale Peabody Museum 1568.—right ilium.

Description: The ilium is a flattened blade, smooth medially, with no indication of a sacral attachment. Dorsally and ventrally there are crests developed, giving a lenticular cross-section. Posteriorly these crests disappear and the cross-section is circular at the tip. Anteriorly there is a prominent crest with a boss laterally for muscle attachment. The acetabular area is broken ventrally and no trace of attachment for pubis or ischium remains. A tiny part of the acetabulum is present.

Discussion: This bone was first discussed by Moodie (1912), p. 287) who indicated that it was "quite peculiar" and would "possibly be sufficiently characteristic to sustain the validity of Professor Marsh's genus *Eobatrachus*." Later (1914, p. 533) he indicated that there were four pits on the articular surface marking the "synchondrosteal union of the halves of the pelvis." These pits are breakage surfaces; no evidence of the actual articular surface remains. Reference of this bone to the Reptilia indicates that it must be the right ilium with the narrow tip pointing posteriorly, rather than the left bone with

anteriorly pointing tip as Moodie suggested. There is a superficial resemblance to raniform frogs, principally due to the size of the dorsal crest, but anuran ilia in general lack the ventral crest and are relatively much longer than this specimen. The short, compressed bladelike shape most closely resembles that of the Sauria. Ili of all families of lizards have been examined, as well as those of other recent and many fossil reptiles. The general shape of the bone conforms most closely among lizards to certain gekkonids (e.g. *Thecadactylus*) but the latter differ in the less well developed dorsal muscular crest. Breakage of the acetabular region renders further comparison fruitless; the primary reason for discussion of the bone here is indication of its reptilian nature.

SUMMARY AND CONCLUSIONS

The type materials of the earliest known North American fossil frog *Eobatrachus agilis* Marsh are redescribed. The holotype of *E. agilis* is a right humerus and the genus is tentatively referred to the Aglossa (Reig 1958). No comparison is possible at this time with *Montsechobatrachus* and family reference is left open. The other anuran humerus associated with the type is distinctly different and is made the type of a new genus and species *Comobatrachus aenigmatis* which is referred to the Neobatrachia (Reig, *ibid*) without family assignment, though it is possible that it is of leptodactyloid relationships. The associated femur is identified as a urodele, *incertae sedis*, described as *Comonecturoides marshi* and a similarity to *Necturidae* noted. The associated ilium is not anuran and is probably that of a lizard or closely related reptile. The distinctive characters of frog humeri and urodele femora are discussed.

Mook (1918) characterized the environment of the Morrison formation as a broad floodplain with abundant running water. Wieland (1925) suggested a temperate to cool climate, while Simpson (1933) favored a warm to tropical climate. Salamanders are primarily North Temperate today and seek cooler, moister habitats. This may indicate a temperate to warm temperate rather than a tropical environment during Morrison time.

ACKNOWLEDGEMENTS

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PLATE 1

Eobatrachus agilis Marsh, type specimen, YPM 1862

- Fig. 1. Ventral view of right humerus
- Fig. 3. Dorsal view of right humerus
- Fig. 5. Medial view of right humerus

Comobatrachus aenigmatis, n. gen., n. sp., type specimen, YPM 1863

- Fig. 2. Ventral view of right humerus
- Fig. 4. Dorsal view of right humerus
- Fig. 6. Medial view of right humerus

Unknown reptile, YPM 1568

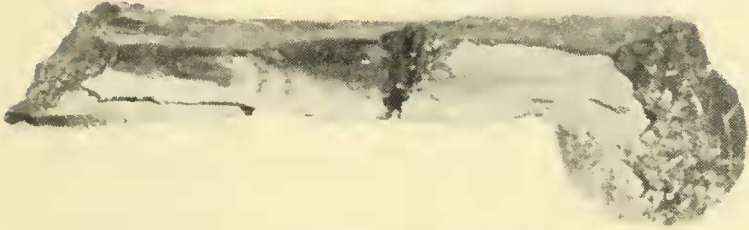
- Fig. 7. Lateral view of right ilium
- Fig. 8. Medial view of right ilium

[Present magnification x 10]

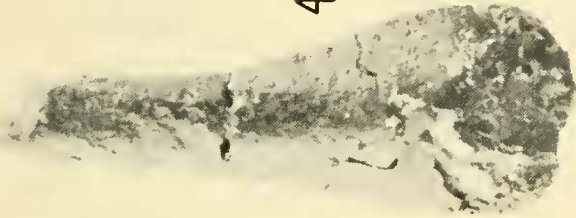
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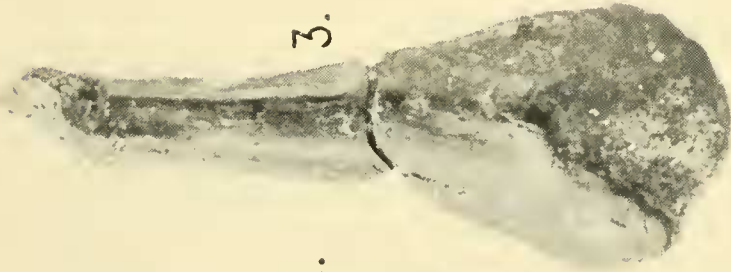
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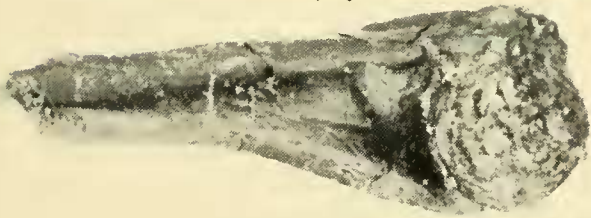
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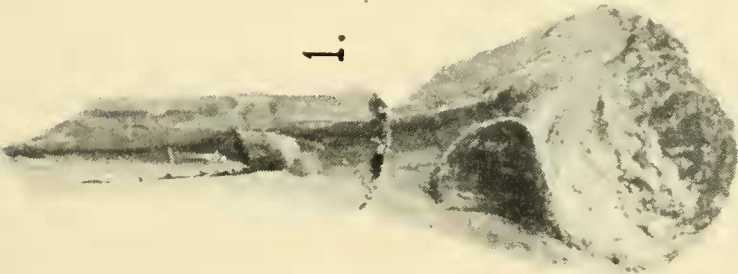
3.



2.



1.



8.



7.



PLATE 2.

Eobatrachus agilis Marsh, type specimen, YPM 1862

Fig. 1. Lateral view of right humerus

Comobatrachus aenigmatis, n. gen., n. sp., type specimen, YPM 1863

Fig. 2. Lateral view of right humerus

Comonecturoides marshi, n. gen., n. sp., type specimen, YPM 3919

Fig. 3. Dorsal view of right femur

Fig. 4. Ventral view of right femur

Unidentified anuran, YPM 1394 (Part of original type of *Eobatrachus agilis*)

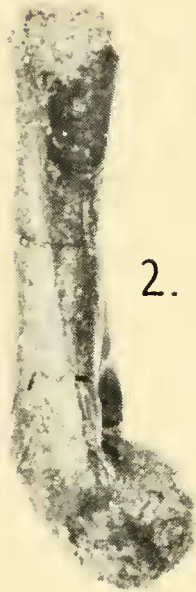
Fig. 5. Dorsal view of distal end of tibiofibula

Fig. 6. Ventral view of distal end of tibiofibula

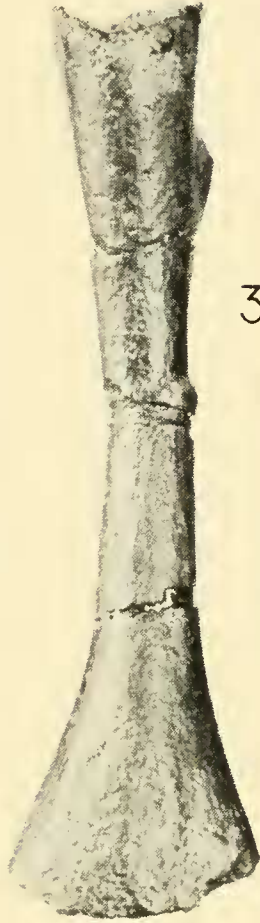
[Present magnification x 10]



1.



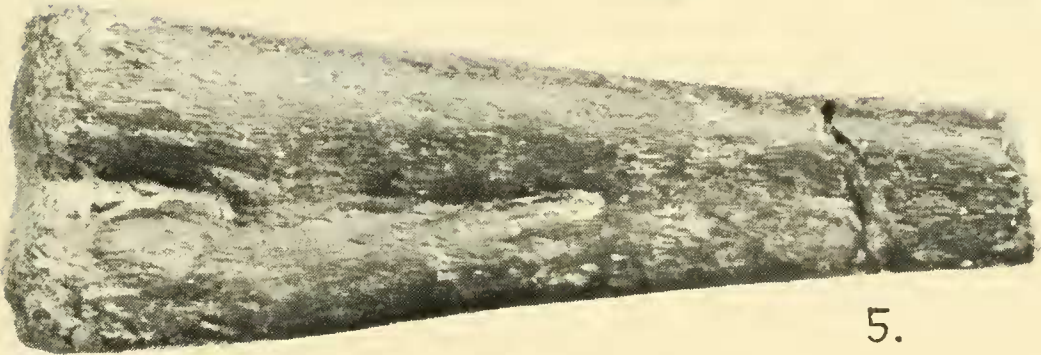
2.



3.



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6.

PLATE 3.

Comparative series of urodele femora. Above: outline of right femur, anterodorsal view. Below: outline of left femoral head in section; the dorsal surface up and the anterior surface to the right. Not to scale.

Fig. 1. Plethodontidae

Fig. 2. Salamandridae

Fig. 3. Proteidae

Fig. 4. Ambystomatidae

1. *Ambystoma*

2. *Dicamptodon*

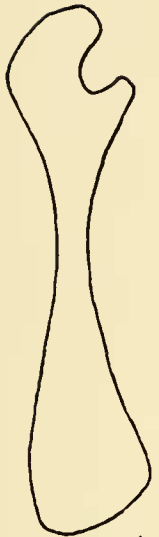
Fig. 5. Hynobiidae

Fig. 6. *Comonecturoides marshi*, n. gen., n. sp

Fig. 7. Necturidae

Fig. 8. Cryptobranchidae

Fig. 9. Amphiumidae



1.



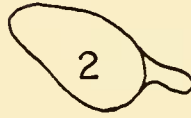
2.



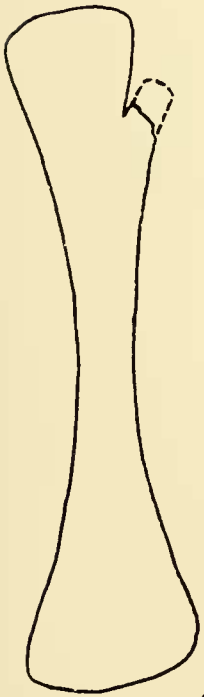
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